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## Biodiversity of plankton and a Chemostat

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Biodiversity has both fascinated and puzzled biologists<sup>1</sup>. In aquatic ecosystems, the biodiversity puzzle is particularly trouble-some, and known as the ‘paradox of the plankton’<sup>2</sup>. Competition theory predicts that, at equilibrium, the number of coexisting species cannot exceed the number of limiting resources<sup>3–6</sup>. For phytoplankton in lakes and marshes, a few resources are potentially limiting: phosphorus or nitrogen<sup>7</sup>. However, an unlimited number of phytoplankton species coexist there<sup>2,7</sup>. Here, we offer a solution to the paradox of the plankton. We build a resource competition model with the crowding effect, where the specific reproduction rate is reduced by crowding.

We discuss a model based on the simplest case of well-known resource competition models<sup>6,8–11</sup> that has been tested and verified extensively using competition experiments with phytoplankton species<sup>9,12–18</sup>. Consider  $n$  species and one resource. Let  $N_i$  denote the population abundance of species  $i$ , and let  $R$  denote the availability of the resource. The dynamics of the species depend on the availability of the resource and the crowding effect caused by their own population density. The resource availability depends on the rate of resource supply and the amount of a

resource consumed by the species. This gives the following model:

$$\begin{aligned}\frac{dN_i}{dt} &= N_i (c_i(N_1, \dots, N_n) \mu_i(R) - d_i) \quad i = 1, 2, \dots, n \\ \frac{dR}{dt} &= D(S - R) - \sum_{i=1}^n \gamma_i \mu_i(R) N_i\end{aligned}\quad (1)$$

Here,  $c_i(N_1, \dots, N_n)$  reflects the crowding effect on the specific growth or reproduction of species  $i$ ;  $\mu_i(R)$  is the specific growth rate of species  $i$  as a function of the resource availability;  $d_i$  is the specific death rate of species  $i$ ;  $D$  is the system's turnover rate;  $S$  is the supply concentration of the resource; and  $\gamma_i$  is the content of the resource in species  $i$ . We assume that the specific growth rates follow the Monod equation<sup>19</sup>, and are determined by  $\mu_i(R) = (r_i R)/(K_i + R)$ , where  $r_i$  is the maximum specific growth rate of species  $i$  and  $K_i$  is the half-saturation constant for the resource of species  $i$ .

For natural phytoplankton communities, crowding may have a negative effect on their own growth or reproduction. It is natural to assume that  $c_i$  is a decreasing function. In the simplest case this would take the form

$$c_i(N_1, \dots, N_n) = \frac{1}{1 + \sum_{j=1}^n \alpha_{ij} N_j}, \quad (2)$$

where  $\alpha_{ij}$  is an intra- (or inter-) specific crowding parameter. The function  $c_i$  becomes identical if  $\alpha_{ij} = 0$  for all  $i, j$ .

What happens if the crowding effect on the specific growth of species  $i$ , respectively, is limited to the case where  $\alpha_{ii} = \alpha_i > 0$  and the other crowding parameters are zero? Let

$$\lambda_i = \frac{K_i d_i}{r_i - d_i} > 0$$

and assume  $\lambda_1 \leq \lambda_2 \leq \dots \leq \lambda_n$  without loss of generality. Then, (1) has a unique stable interior equilibrium if and only if  $\lambda_n < S$  and  $R_{i-1}^* > \lambda_i$  ( $i = 2, 3, \dots, n$ ) hold, where  $R_{i-1}^*$  represents the  $R$  component of the coordinates of an interior equilibrium for a subsystem  $(R, N_1, \dots, N_{i-1})$  (the proof is not shown).  $\frac{K_i d_i}{S(r_i - d_i)}$  is the break-even concentration of species  $i$ <sup>25</sup>. We here call it as the *crude* break-even concentration of species  $i$ .  $\lambda_i$  is then called the *net* break-even concentration of species  $i$ , which is its crude break-even concentration multiplied by the supply concentration of the

resource. The case  $n = 2$ , that is, the case where two species and one resource are considered, implies permanence as well as stability at a unique interior equilibrium (the proof is also not shown). For more general case of (2), we can confirm a situation in which a stable interior equilibrium exists (not shown). This makes us predict that permanence holds for numerous species and more general case of (2). Crowding effects caused by the population density at the specific reproduction level allow the robust coexistence of an unlimited number of species for a single limiting resource.

It is known that competition models with the crowding effect (or intraspecific interference) on the growth of species enable the stable coexistence of many species for homogeneous resources that reproduce by themselves<sup>26–34</sup>. Also, it was reported that the paradox of the plankton was solved by considering the non-equilibrium dynamics on three or more nutrients<sup>12</sup>. What is new here is that we found the mathematically ensured stable coexistence situation of an unlimited number of species in a competition model even for a single nutrient resource that does not reproduce by itself. The model is based on the simplest case with the crowding effect at the specific reproduction level. In general, the limiting nutrient resource to phytoplankton species in lakes and marshes is phosphorus or nitrogen<sup>7</sup>; at most two limiting resources. Moreover, the non-equilibrium dynamics cannot lead the robust coexistence of species even if oscillations and chaos in species abundances allow the coexistence of many more species than limiting resources<sup>12</sup>. Without the robust coexistence of species, it may be hardly possible that natural phytoplankton communities have survived against some environmental fluctuations. Our results state that the robust coexistence occurs whenever each species has self-inhibitory (in its reproduction) well-balanced to the resource. That is biologically realistic; such competitors indeed occur in real-world plankton communities. We conclude that the biodiversity of plankton communities need neither be explained by external factors<sup>12,14,21–23</sup> nor come from the competition process itself on three or more nutrients<sup>12</sup>, but could be based on the crowding effect to their own growth at the specific reproduction level. Once a plankton community has the well-balanced crowding effect to its own population growth, the number of coexisting phytoplank-

ton species can greatly exceed the number of limiting resources, even for a single limiting resource and even in a constant and well-mixed environment. In this sense, the paradox of the plankton is solved essentially.

These findings have some wider implications that go beyond the plankton systems studied here. First, within the biological realm, our explanation for planktonic biodiversity may serve as a conceptual model for the biodiversity of many other ecosystems as well. For example, water flea and yeast fungi, which are not phytoplankton species, have a density dependence effect, that is, inhibitory to the population growth at their reproduction level<sup>35,36</sup>. Second, our results do not follow competition experiments with phytoplankton species<sup>9,13-18</sup>. This may come from the reason why the ideal environment of experiments ignores process that affects inhibitory in the population growth (caused by the population crowding) at the specific reproduction level. In real-world plankton communities, crowding has a direct or indirect effect negative to their own reproduction, such as, for example, an enzymatic inhibitor or wastes, respectively. Wastes accumulated around species will lead to a shortage of essential substances to the life activities of the species, for example, oxygen and carbon dioxide (these are not included in resource nutrients). That should affect inhibitory in the population growth at the reproduction level. These will await the results of coming research and experiment. Third, our results show that competition on limiting resources less than three kinds is not necessarily a destructive force. Competitive interactions that have crowding effects caused by the population density at the specific reproduction level can allow the robust persistence of a great diversity of competitors on a single limiting resource or a couple of limiting ones.

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